

## PELAGE OF HYBRID GIBBONS (*HYLOBATES LAR* × *H. PILEATUS*) OBSERVED IN KHAO YAI NATIONAL PARK, THAILAND

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### A B S T R A C T

The pelages of 12 wild hybrid gibbons in the zone of contact between *Hylobates lar* and *H. pileatus* in Khao Yai National Park, central Thailand, are described and illustrated in color. The hybrids include adults of both sexes with intermediate pelage, individuals with *lar*-like or *pileatus*-like pelage and immatures that are known backcrosses to *lar*. Hybrid coloration, especially on the face, is quite variable but most animals tend to have dark fronts and buff or grayish-backs and some white on the eyebrows, reminiscent of the coloration of *Hylobates muelleri* on eastern Borneo.

### I N T R O D U C T I O N

Three species of gibbons occur in Thailand: *Hylobates lar* in the north, west and south, *H. pileatus* in the southeast and *H. agilis* in parts of the far south near the Malaysian border (FOODEN, 1971; MARSHALL et al., 1972; MARSHALL, 1981). These species plus two others (*H. muelleri* of Borneo and *H. moloch* of Java) make up the 'lar group', five closely related forms that are very similar anatomically (CREEL & PREUSCHOFT, 1984) and which are distributed allopatrically over the Sunda Shelf (GROVES, 1972; CHIVERS, 1977; BROCKELMAN & GITTINS, 1984; MARSHALL & SUGARDJITO, 1986). These five forms often interbreed in captivity, producing hybrid offspring. Nevertheless, they can be readily distinguished by features of pelage and voice (MARSHALL & MARSHALL, 1976; BROCKELMAN & SCHILLING, 1984; MARSHALL & SUGARDJITO, 1986) and therefore are best considered separate species. Typical species characters do not vary clinally, but extend right up to the rivers and straits that form the barriers between species.

Studies of species' interactions in three areas where species come into contact in the headwaters of rivers (the Takhong in Northeast Thailand, the Mudah in northern peninsular Malaysia and the Barito in Kalimantan) have provided evidence that the five forms of lar gibbons do not interbreed freely, but maintain largely separate gene pools in areas of narrow sympatry (BROCKELMAN, 1978; BROCKELMAN & GITTINS, 1984; MARSHALL & SUGARDJITO, 1986). Nevertheless, evidence for some hybridization has been found in all three areas studied. In the zone of sympatry in Khao

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Yai, which has received the most study, about 25 adult hybrids have been identified on the basis of both pelage coloration and voice, and these constitute 5 percent of the breeding population surveyed. Individuals with hybrid characteristics have not been found more than 9 km from the center of the contact zone which is located about a line passing somewhat east of the Tourist Authority bungalows to north of Heiwa Suwat Falls.

*H. lar* and *H. pileatus* are the most easily distinguishable of the five forms to meet in a contact zone. The fact that some hybridization occurs despite the distinctness of the pelage and sex-specific vocal patterns that are probably important in mate recognition and pair bonding is attributed to their previous divergence in separated areas and the lack of selection for behaviors that would prevent hybridization and lack of reinforcement of species differences where they now come into contact.

Although the hybrids appear to be healthy and vigorous and are usually fertile, this does not necessarily imply that they are as fit (successful in leaving progeny) as normal *lar* and *pileatus*, or that significant genetic exchange between the species is occurring. Elsewhere we have described the disruption of normal social behavior which occurs in some mixed species groups and presented some evidence that pair bonds between unlike types are not as stable as they should be (BROCKELMAN & SRIKOSAMATARA, 1984; MARSHALL & SUGARDJITO, 1986); both of these factors would reduce the reproductive success of hybrids and reduce or prevent exchange of genes between the species across the contact zone. Thus, despite the existence of hybrids, the contact zone may represent a "genetic sink" which prevents passage of genes from one species outward into the other. Only more long term and more quantitative observations on behavior will fully answer this question. Unfortunately, it is not feasible at present to catch the animals to sample biochemical characteristics without undue risk of mortality and disruption of social relationships.

In this report we describe and comment on the pelage features of some hybrid gibbons in Khao Yai. Some of these animals are still on their territories, but others have apparently disappeared. The pelage characteristics of all individuals have been listed in BROCKELMAN & GITTINS (1984), and sonograms of the songs of several have been analyzed from tape recordings and published (BROCKELMAN & SCHILLING, 1984; MARSHALL & SUGARDJITO, 1986).

## METHODS

We have taken detailed notes on the pelage features of all gibbons observed in the *H. lar* — *H. pileatus* contact zone since the first observations were made around 1967. Gibbons were observed carefully with 7X or 10X binoculars; all were studied on several occasions. We present watercolors of 12 of these individuals painted by JTM, based on our combined notes and sketches done in the forest. Some paintings (KSI female,

Table 1. List of hybrid gibbons illustrated (ad., adult; juv., juvenile; s.a., subadult).

Group	Age, sex	Location	Year first observed	Comments
TO1	ad. F	571948	1974, 1975	very <i>lar</i> -like
K12	ad. F	532000	1978	<i>lar</i> -like
HE2	ad. F	572976	1977	<i>lar</i> -like
CW6	juv. F	582997	1978	backcross to <i>lar</i>
CW6	ad. F	582997	1978	intermediate
CW10	ad. F	574990	1977	intermediate
TO2	ad. F	573943	1975	intermediate
KS1	s.a. F	597933	1978	somewhat <i>pileatus</i> -like
CW2	ad. M	585999	1977	<i>lar</i> -like
CW10	ad. M	574990	1977	intermediate
HS1	ad. M	602972	1972, 1977	intermediate
CW6	s.a. M	582997	1978	backcross to <i>lar</i>

KI2 female, CW6 and CW10 individuals) are based on only WYB's field notes and face sketches, and were retouched following critical comments by him.

Each group is designated by two letters (indicating a particular area of the contact zone) followed by a group number (Table 1, Fig. 1). The location of the approximate center of each group's territory can be found to within 100 m on 1:50,000 Royal Thai Survey Dept. Sheet 5237 I (Ban Salika), Series L7017, from the 6-digit grid coordinates listed in Table 1 (read right, then up).

The parents of the various territorial adult hybrids in Khao Yai are not known with the exception of one male (SY1), which was originally seen as an infant being carried by a *lar* female which was mated to a *pileatus* male. This F1 male has been tape recorded but not yet painted or photographed. We can roughly infer the proportion of *lar* and *pileatus* ancestry in female hybrids, however, from analysis of sonograms of recorded great-calls sung during duets. The great-call is an extended and highly stereotyped series of hoots with a pattern determined by the animal's genes with little, if any, modification by learning (BROCKELMAN & SCHILLING, 1984; GEISSMANN, 1984; TENAZA, 1985). The great-calls of *lar* and *pileatus* are roughly similar in length (usually 15–20 sec.) but in *lar* they have 7 to 12 notes (average 9), lasting about 2 sec., whereas in *pileatus* there are around 60–80 notes reaching a maximum tempo of around 9.5–10.0 notes per sec. during the trilled end of the call. Two known F1 female hybrids between *lar* and *pileatus* in European zoos have great-calls reaching maximum tempos of 2.6 and 2.9 notes per sec. (BROCKELMAN & SCHILLING, 1984). Based on this information, as well as pelage features, we have inferred that Khao Yai adult females

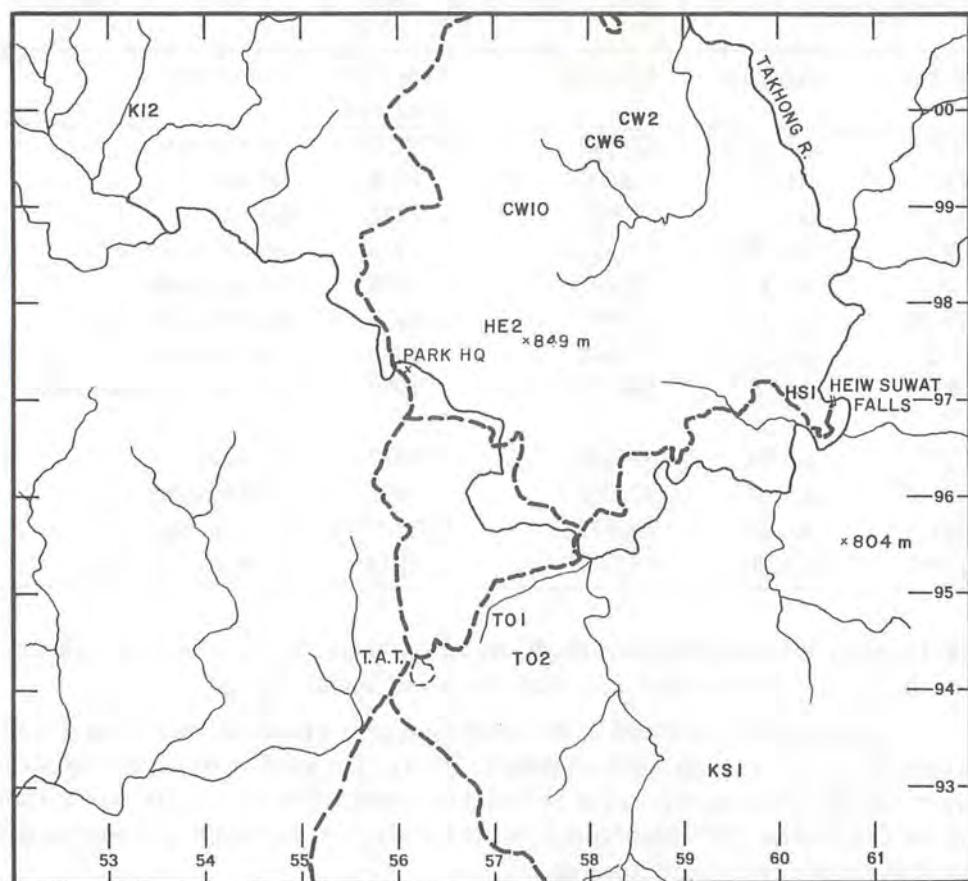


Figure 1. Map of *Hylobates lar* — *H. pileatus* contact Zone in Khao Yai Park showing locations of groups with hybrids. Grid lines are 1 km apart and refer to 1:50,000 Sheet 52371. Heavy dashed lines are paved roads.

CW6, CW10, TO2 and possibly KS1 are F1 hybrids or have approximately equal numbers of *lar* and *pileatus* genes. Other individuals are known or inferred to be backcrosses to *lar* or *pileatus*, as indicated in Table 1. The males have also been inferred to be intermediate or more *lar*-like or *pileatus*-like based of their resemblance to the SY1 male in pelage and voice, and to certain F1 males we have seen in zoos.

#### DESCRIPTIONS

##### *Typical lar*

Fig. 2 shows a light phase male and a dark phase female typical of the subspecies

*entelloides* which we believe occurs in Khao Yai (BROCKELMAN, 1985). Color phase is not sex-linked — either sex may be either phase — and no color discrimination seems to occur in pairing. No color changes occur during growth and maturation except for a narrowing of the face ring. The light phase is often darker buff or more tan than shown in the plate. The dark phase may be a very dark brown, brownish-black or off-black, but rarely as black as male *pileatus*. The dark phase often appears less dark in direct sunlight, and the animals must be observed on several days under various light conditions. There is no body pattern or variation in shade between front and back. The complete white face ring, uniform in width, is a good species identification character. Juveniles usually have more ample white around the face, especially of the cheeks. In very light buff individuals the face ring may be barely distinct.

#### *Typical pileatus*

Sexually dichromatic (Fig. 3); females buff-gray (often more buff than shown in plate) with black cap, throat, the black front narrowing to the groin. Juveniles have white encircling the face, but at maturity this is reduced to white eyebrows, with some white on the sides, barely reaching the chin. In older females the eyebrows become reduced in size and in aged females there may be no white hairs remaining on the face at all. Older females also seem to have more black on the neck and cheeks and have elongated tufts of light hairs over the ears which fall down beside the face.

Juveniles all have coloration similar to mature females but at maturity males turn all black except for white eyebrows, streaks of light hairs extending from the corners of the eyebrows back along the sides of the crown (the corona), a flashy white tuft of fur covering the scrotum and whitish hands and feet.

Both sexes have hairs somewhat flattened against the crown.

#### *Female hybrids, lar-like*

The TO1 female (Fig. 4) was first considered to be a *lar*, but later we decided that she was atypical, having too much white extending from the hands up the forearms, and a great-call slightly too fast. She is possibly a 2nd generation backcross.

The CW6 female juvenile, about 4 years old when first observed, is the daughter of a female hybrid and *lar* male, and is probably a 1st generation backcross. Her chest is nearly black, upper back blackish but lower back dark buff; upper (proximal) parts of arms and legs blackish but lower extremities tending toward light buff. Top of head black, grading to dark buff on neck; face ring luxuriant, with double tufts near ears.

The KI2 female (Fig. 5), the farthest west hybrid found, was recorded and seen in 1977-78 but has not been checked since: Upper back grayish-black, grading to blackish-buff at the waist; front black and not sharply demarcated from back; head very dark, face ring consisting only of narrow eyebrows and a slight line under the chin. Mated with a buff *lar*; two *lar*-like juveniles in the group.

The HE2 female (Fig. 5), on the northwest side of Hill 849 east of park headquarters, is brownish black with a grayish rump; face ring not very distinct under chin. Two offspring were present when last seen in 1978; heard in subsequent years and may still be present.

The great-calls of KI2 and HE2 suggest about 3/4 *lar* genes.

#### ***Female hybrids, intermediate***

The CW6 adult female (Fig. 6) was blackish tinged with buff, with front nearly black and not sharply divided from back. Proximal and inner surfaces of extremities nearly black, outer parts brown, and lower thirds tending toward white. Head black and furry-looking, no ear tufts, eyebrows white but rather narrow. A vigorous female who sang often; discovered in 1977 but disappeared from territory during 1980-81.

The CW10 female (Fig. 6) was blackish with silvery or buff cast on back, buff-black lower back and thighs, blackish front; face ring consisted of narrow white semi-circles part way around eyes. Seen in 1977 with grayish infant about 2½ years; mated with male hybrid. Rediscovered in neighboring territory with new *lar* mate in 1982.

The TO2 female, who lived for many years about ½ km east of the Tourist Authority bungalows, had a dark front, buff-gray on lower back, arms and legs, dark shoulders, nearly black head with indistinct face ring. This robust and active female, mated to a *pileatus*, was first heard in 1972 and disappeared from its territory in 1978, when it apparently moved about 1 km to the southeast.

The KS1 female (Fig. 6 and cover) is somewhat more *pileatus*-like than those described above: back buff, upper chest blackish, lower chest and abdomen lighter; front more sharply bordered than those above; upper parts of extremities dark, tending to whitish distally; black cap, cheeks dark, eyebrows off-white or light buff, sides of head buff. When discovered in 1978 this female was part of a group with *pileatus* male and buff *lar* female adults and sang during their duets as a daughter normally does. Her somewhat *pileatus*-like pelage and song, however, casts some doubt on her status as an F1 hybrid daughter of this group.

A more *pileatus*-like hybrid, CW15, is pictured in Plate 2 of MARSHALL & SUGARDJITO (1986).

#### ***Male hybrids***

The HS1 hybrid male (Fig. 6) was black like *pileatus* with white on hands and feet, scrotum, and a face ring complete but wider on the eyebrows than around the bottom. Hairs appressed to the head in *pileatus* fashion, but no noticeable corona. This was the first hybrid to be found, in 1972 by JTM (before we realized that we were

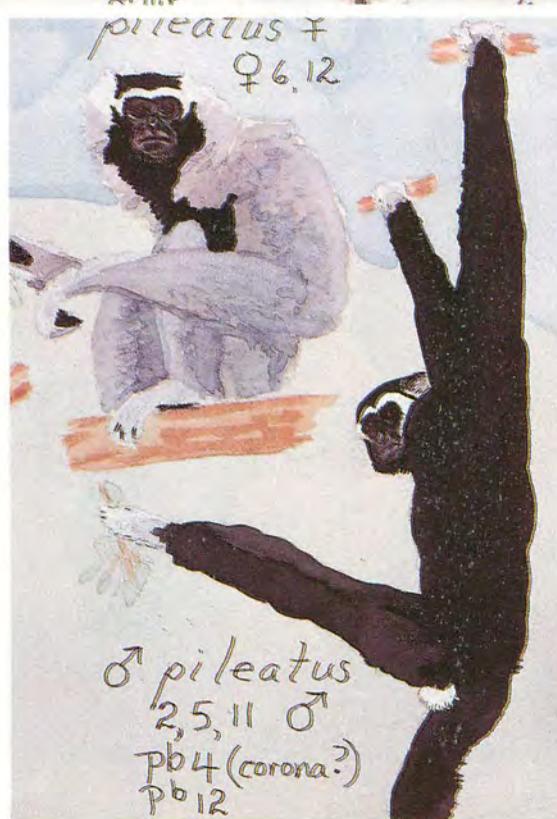


Figure 2. Light phase and dark phase *Hylobates lar entelloides* from Khao Yai National Park.  
Figure 3. Female (upper left) and male (right) *Hylobates pileatus*.

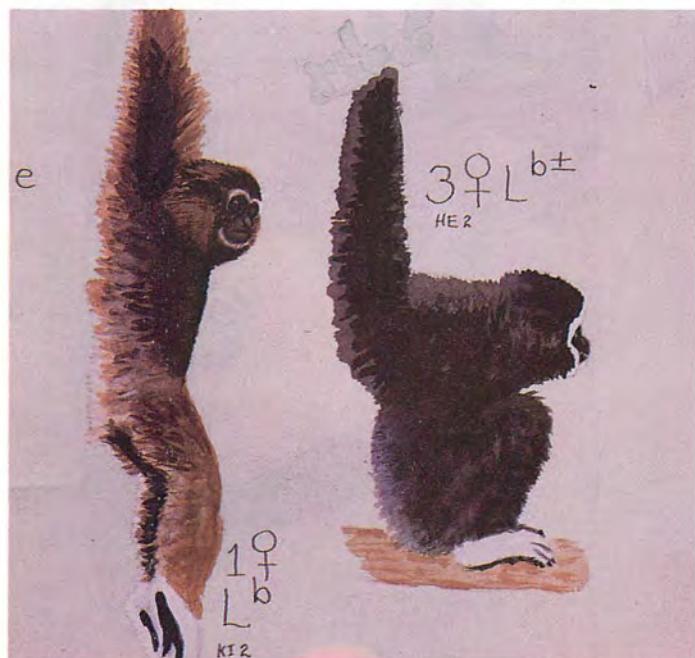


Figure 4. Hybrid gibbons in Khao Yai. Left : TO1 *lar*-like female; right: CW6 juvenile female.  
Figure 5. Hybrids in Khao Yai. Left: KI2 female; right: HE2 *lar*-like female.



Figure 6. Hybrid gibbons in Khao Yai. Upper left: HS1 male; upper right: CW10 male (eyebrows should be bushier and less distinct); left middle: CW6 adult female; center: CW10 adult female; lower right: KS1 subadult *pileatus*-like female; lower left: TO2 female.



Figure 7. Male hybrid gibbons in Khao Yai. Left: CW2 adult male; Right: CW6 subadult male, backcross to *lar*.

Figure 8. Bornean gibbons. Left: *Hylobates agilis albifrons* male from southwest Kalimantan; right: *Hylobates muelleri* male from eastern Kalimantan.

seeing and hearing hybrids in Khao Yai). WYB observed it well in 1977, but could not find it in 1983 or later.

CW10 (Fig. 6), the former mate of the CW10 female hybrid, was intermediate between *lar* and *pileatus* in most respects with black pelage, somewhat indistinct grayish-white eyebrows and grayish-white scrotal tuft.

CW2 (Fig. 7) was a very black *lar*-like hybrid with a peculiar '3-ring' face ring; scrotum not noted, voice *lar*-like with some peculiar phrases.

The CW6 subadult male had a broad face ring (with lateral tufts reminiscent of *pileatus*) typical of young animals; body brownish black, cap black and somewhat flattened; pubic region, including scrotum, brownish buff. This male evidently had a hybrid mother and a *lar* father.

#### DISCUSSION

No two individual hybrids are exactly the same in the zone of contact in Khao Yai. Their individuality is probably most marked in their facial patterns. Some individuals have complete or nearly complete face rings and others have only eyebrows or partial circlets of white around the eyes. Part of this variation, of course, could be due to age changes. Body color varies from tan or buff to black; there is no solid brown color. Intermediate shades appear silvery or buffy black, as if body hairs were black proximally and buff or grayish distally. Most *lar*-like or intermediate hybrids are rather dark have found no hybrid that is clearly 'light phase'. Body coloration also tends to be patterned somewhat like *pileatus*, with dorsal surfaces tending to be lighter than ventral surfaces, but with lower back and thighs tending to be lighter than the upper back, and distal parts of limbs lighter than more proximal parts (this has not been emphasized sufficiently in many of the plates).

The coloration of hybrids is less uniform and predictable than their vocal patterns, which in the number of notes, final tempo reached and in certain other more subtle features, vary quantitatively along a single gradient from *lar* to *pileatus* (BROCKELMAN & SCHILLING, 1984; in a future report we will analyze and compare quantitatively the song patterns of all available hybrids). This suggests that pelage is controlled by many interacting genetic loci, whereas song pattern is controlled by several alleles and loci with additive effects.

It has been remarked that the pelage of hybrids resembles that of certain types of Bornean gibbons, especially *H. muelleri* from eastern Kalimantan (MARSHALL & SUGARDJITO, 1986). Two types of Bornean gibbons appear in Fig. 8: *H. agilis albobarbis* of southwest Kalimantan and *H. muelleri muelleri* from the east. Note the dorsal-ventral difference in color, eyebrows and dark caps. Both Bornean gibbons pictured have dark hands and feet, which contrasts with all *lar* and *pileatus*. Resemblance of Khao Yai hybrids to Bornean gibbons may be more than coincidence;

it has been suggested that Borneo was the center of origin of the lar species group (CHIVERS, 1977). *H. muelleri* also shows the greatest regional differentiation in pelage characteristics (KLOSS, 1929; GROVES, 1971), which is consistent with its having occupied its present range for the longest period of time.

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#### R E F E R E N C E S

BROCKELMAN, W.Y. 1978. Preliminary report on relations between the gibbons *Hylobates lar* and *H. pileatus* in Thailand. Pages 315-318 in D.J. Chivers and K.A. Joysey (eds.), *Recent Advances in Primatology*, vol. 3. Academic Press, London.

BROCKELMAN, W.Y. 1985. A gibbon pelt (*Hylobates lar entelloides*) from Khao Yai National Park, Saraburi Province, Thailand. *Nat. Hist. Bull. Siam Soc.* 33: 55-57.

BROCKELMAN, W.Y. and S.P. GITTINS. 1984. Natural hybridization in the *Hylobates lar* species group: implications for speciation in gibbons. Pages 498-532 in H. Preuschoft, D.J. Chivers, W.Y. Brockelman and N. Creel (eds.), *The Lesser Apes: Evolutionary and Behavioural Biology*. Edinburgh Univ. Press, Edinburgh.

BROCKELMAN, W. Y. and D. SCHILLING. 1984. Inheritance of stereotyped gibbon calls. *Nature* 312: 634-636.

BROCKELMAN, W.Y. and S. SRIKOSAMATARA. 1984. Maintenance and evolution of social structure in gibbons. Pages 298-323 in H. Preuschoft, D.J. Chivers, W.Y. Brockelman and N. Creel (eds.), *The Lesser Apes: Evolutionary and Behavioural Biology*. Edinburgh University Press, Edinburgh.

CHIVERS, D.J. 1977. The lesser apes. Pages 539-598 in Prince Rainier and G. Bourne (eds.), *Primate Conservation*. Academic Press, New York.

CREEL, N. and H. PREUSCHOFT. 1984. Systematics of the lesser apes: a quantitative taxonomic analysis of craniometric and other variables. pages 562-613 in H. Preuschoft, D.J. Chivers, W.Y. Brockelman and N. Creel (eds.), *The Lesser Apes: Evolutionary and Behavioural Biology*. Edinburgh Univ. Press, Edinburgh.

FOODEN, 1971. Report on primates collected in western Thailand, January-April 1967. *Fieldiana Zoology* 59: 1-62.

GEISSMANN, T. 1984. Inheritance of song parameters in the gibbon song, analyzed in 2 hybrid gibbons (*Hylobates pileatus* X *H. lar*). *Folia Primatol* 42: 216-235.

GROVES, C.P. 1971. Geographic and individual variation in Bornean gibbons, with remarks on the systematics of the subgenus *Hylobates*. *Folia Primatol.* 14: 139-153.

GROVES, C.P. 1972. Systematics and phylogeny of gibbons. Pages 1-89 in D.M. Rumbaugh (ed.), *Gibbon and Siamang*, vol. 1. Karger, Basel.

KLOSS, C.B. 1929. Some remarks on the gibbons, with the description of a new subspecies. *Proc. Zool. Soc. London* 1929: 113-127.

MARSHALL, J.T. 1981. The agile gibbon in south Thailand. *Nat. Hist. Bull. Siam Soc.* **29**: 129-136.

MARSHALL, J.T. and E.R. MARSHALL. 1976. Gibbons and their territorial songs. *Science* **193**: 235-237.

MARSHALL, J.T., B. ROSS and S. CHANTAROJVONG. 1972. The species of gibbons in Thailand. *J. Mammal.* **53**: 479-486.

MARSHALL, J. and J. SUGARDJITO. 1986. Gibbon systematics. Pages 137-185 in D. Swindler (ed.), *Comparative Primate Biology, vol. 1: Systematics, Evolution and Anatomy*. Alan R. Liss, New York.

TENAZA, R. 1985. Songs of hybrid gibbons (*Hylobates lar* X *H. muelleri*). *Amer. J. Primatol.* **8**: 249-253.

